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Morphology of the megalopal stage of *Chasmagnathus granulatus* Dana, 1851 (Crustacea: Decapoda: Brachyura: Varunidae), with comments on morphological anomalies

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Abstract.—Megalopal morphology of *Chasmagnathus granulatus* Dana was studied in field-collected specimens from Mar Chiquita Lagoon and Samborombón Bay, Argentina. Characters overlooked in a previous description of laboratory-reared specimens, such as the cephalothoracic dorsal setation, maxillule, maxilla, sternum, and abdominal dorsal setation, are examined. In agreement with zoeal morphology, several characters observed in these megalopae indicate that *C. granulatus* belongs to the family Varunidae, instead of the Sesarmidae. These include presence of the antennular endopod, presence of an epipod on the second maxilliped, number of the antennal flagellum segments, and the setation patterns of the mandibular palp, pleopods, and uropods. Some anomalous megalopae, bearing modified zoeal characters, were also encountered. Some megalopae exhibited lateral spines on the carapace, rudiments of exopod and protopod on the antennular peduncle, a modified endopod and exopod of first maxilliped, and rudiments of furcae on the telson. The latter findings are discussed in terms of the variability in brachyuran larval development.

The early life history of brachyuran crabs includes a zoeal and megalopal phase, the latter a morphologically unique phase intermediate between planktonic zoeae and benthic adults. The systematics of the Brachyura has traditionally been based on adult morphology, although some recent studies using zoeal and/or megalopal morphology support changes in classification (Rice 1988, Clark & Webber 1991, Cuesta 1999, Clark & Ng 2000). However, only thorough descriptions of larval stages allow subsequent analysis. Some old descriptions do not meet modern standards for descriptions and illustrations of appendages, and even good descriptions may now be deemed incompletes, especially given the necessity for detailed information (e.g., setation) as is provided by means of new optical devices and the standardization of procedures and techniques (Clark et al. 1998). Consequently, a number of species already described must be redescribed in more detail.

Southwestern Atlantic saltmarshes are characterized by dense populations of *Chasmagnathus granulatus* Dana, 1851 (often incorrectly referred to as *C. granulata*), a semiterrestrial burrowing grapsoid crab (Spivak 1997). The life cycle of *C. granulatus* includes four or occasionally five zoeae and one megalopa (Boschi et al. 1967, Pestana & Ostrenski 1995). In the present study a re-examination and redescription of the megalopal stage of *C. granulatus,* from field-collected material, is provided in order to clarify morphological features now used in higher classification and to determinate setation patterns of different appendages for comparisons with megalopae of related genera.

Materials and Methods

Megalopae were collected in two temperate estuaries of the Argentine coast: Samborombón Bay (36°20′S) and Mar Chiquita Lagoon (37°60′S). At the first site, a plankton net (mesh 300 μm) was towed, and in the second an ad hoc collector was used. All the material collected was preserved in formalin 4%. Appendages were dissected under a Wild MZ6 binocular microscope. Drawings were made using a Zeiss Axioskop microscope equipped with Nomarski interference contrast and attached camera lucida. Drawings were based on five megalopae. The following measurements were taken (±0.01 mm) on 54 Mar Chiquita and 25 Samborombón megalopae with a micrometer eyepiece: cephalothorax length, from the base of the rostrum to the posterior margin; cephalothorax width, as the maximum distance between lateral margins; maximum height and length of the propodus of chelipeds; and first pleopod length. Descriptions and figures are arranged according to the standards proposed by Clark et al. (1998).

Results

Chasmagnathus granulatus Dana, 1851 Megalopa Figs. 1–5

Previous description.—Boschi et al. (1967): 36–39, figs. 11–17.

Cephalothorax (Fig. 1A, B, Table 1).—Longer than broad. Rostrum ventrally deflected (approximately 90°) with a medium cleft. Setal arrangement as figured.

Antennule (Fig. 2A). —Peduncle 3-segmented with 4, 3, 1 setae respectively. Endopod unsegmented with 1 subterminal and 3 terminal setae. Exopod 4-segmented with 0, 3, 4 and 4 aesthetascs, and 0, 0, 2, 2 (1 long plumose) setae respectively.

Antenna (Fig. 2B).—Peduncle 3-segmented with 5, 2, 2 setae respectively. Flagellum 7-segmented with 0, 0, 4, 1, 4, 3, 3 (terminal) setae respectively.

Mandible (Fig. 2C).—Palp 3-segmented, distal segment with 8 (1 subterminal, 7 terminal) setae.

Maxillule (Fig. 2D).—Coxal endite with 18 (1 basal) plumodenticulate setae. Basial endite with 19 (3 basal) plumodenticulate setae. Endopod unsegmented with 6 setae, 2, 2 subterminal and 2 terminal. Exopodal and epipodal setae present; protopod with 2 long setae.

Maxilla (Fig. 2E).—Coxal endite bilobed with 14 + 7 plumodenticulate setae. Basial endite bilobed with 10 (2 inner) + 11 (1 inner) plumodenticulate setae. Endopod unsegmented with 2 setae on low external margin. Scaphognathite with 50 plumose marginal setae and 5 lateral setae (3 on the upper part and 2 in the lower).

First Maxilliped (Fig. 3A). —Epipod with 8 long setae. Coxal endite with 12 plumodenticulate setae. Basial endite with 13 plumodenticulate setae. Endopod unsegmented with 3 simple subterminal setae. Exopod 2-segmented, proximal segment with two distal plumodenticulate setae, distal segment with 4 long terminal plumose feeding setae.

Second Maxilliped (Fig. 3B).—Epipod short with 5 long setae. Coxa and basis not differentiated, with 2 plumodenticulate setae. Endopod 5-segmented, ischium, merus, carpus, propodus and dactylus with 1, 1, 1, 6 and 9 plumodenticulate setae respectively. Exopod 2-segmented, proximal with one medial setae and distal segment with 5 long terminal plumose feeding setae.

Third Maxilliped (Fig. 3C).—Epipod elongated with 20 long setae and 11 long plumodenticulate setae proximally. Coxa and basis not differentiated with 19 plu-

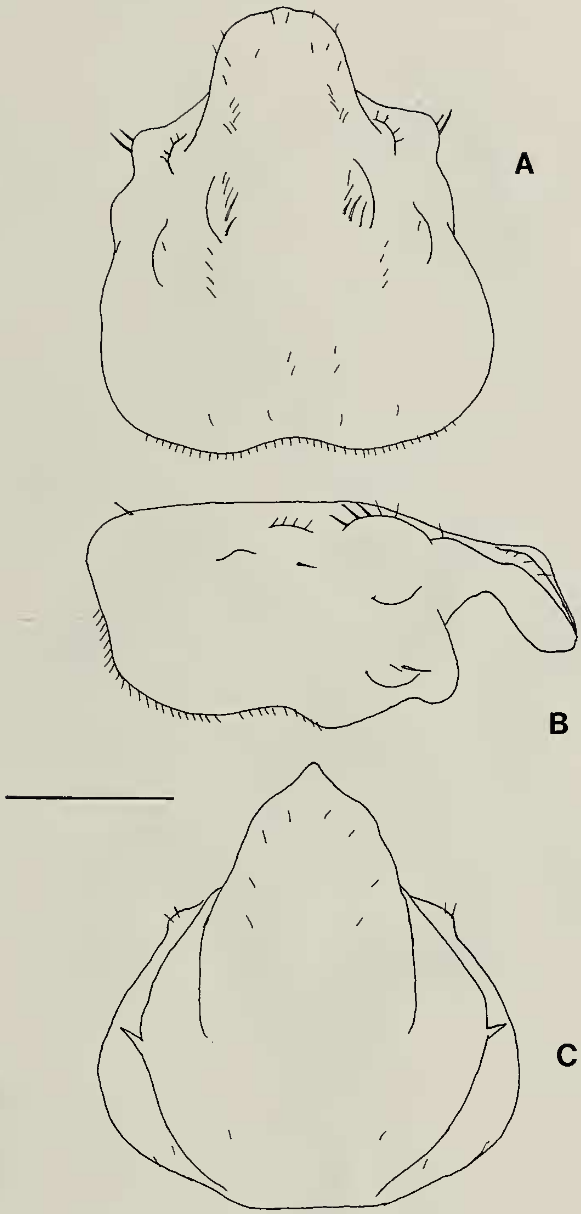

Fig. 1. *Chasmagnathus granulatus* Dana, 1851. Megalopa, cephalothorax. A, dorsal view; B, lateral view; C, anomalous, dorsal view. Scale bar = 0.5 mm.

modenticulate setae. Endopod 5-segmented, ischium, merus, carpus, propodus and dactylus with 14, 11, 8, 8 and 8 plumodenticulate setae respectively. Exopod 2-segmented, proximal segment with 2 medial setae, and distal segment with 5 long terminal plumose raptatory setae.

Pereiopods (Fig. 4B–F). —All segments well differentiated and with setae as figured. Propodus of pereiopods 2–4 with a terminal inner spine. Dactylus of pereiopod 5 with 3 long subterminal setae.

Sternal plate (Fig. 4A).—Setation as figured.

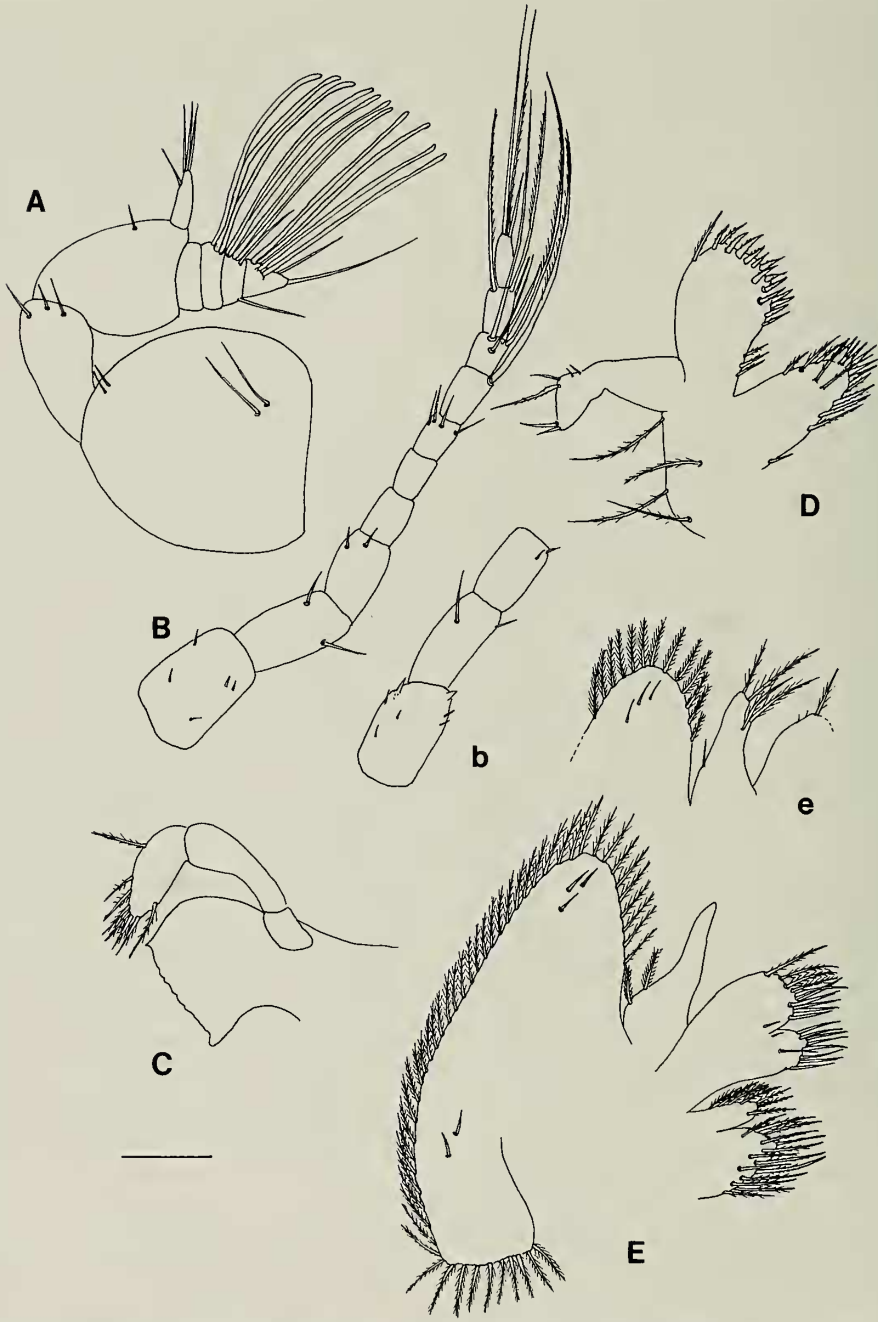

Fig. 2. *Chasmagnathus granulatus* Dana, 1851. Megalopa. A, antennule; B, antenna, b, anomalous antenna (detail); C, mandible; D, maxillule; E, maxilla, e, anomalous maxilla (detail). Scale bar = 0.1 mm.

Abdomen (Fig. 5A).—Six somites present. Somite 1 with 2 pairs of posterolateral setae and 11 mid-dorsal simple setae. Somite 2 with 4 pairs of posterolateral setae and 3 pairs of mid-dorsal setae. Somite 3 with 4 pairs of posterolateral setae. Somite 4 with 3 pairs of posterolateral setae. Somite 5 and 6 with 2 pairs of posterolateral

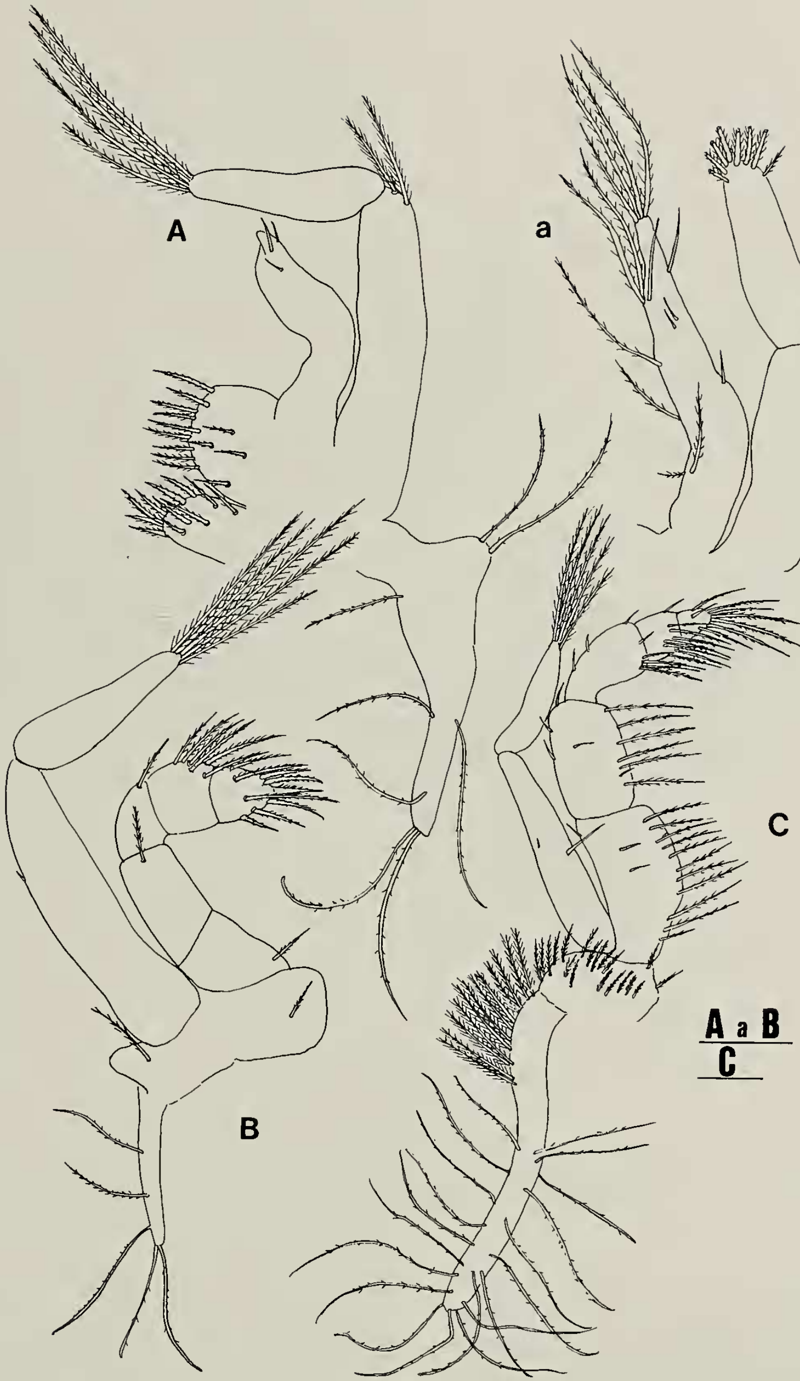

Fig. 3. *Chasmagnathus granulatus* Dana, 1851. Megalopa. A, first maxilliped; a, anomalous first maxilliped (detail); B, second maxilliped; C, third maxilliped. Scale bars = 0.1 mm.

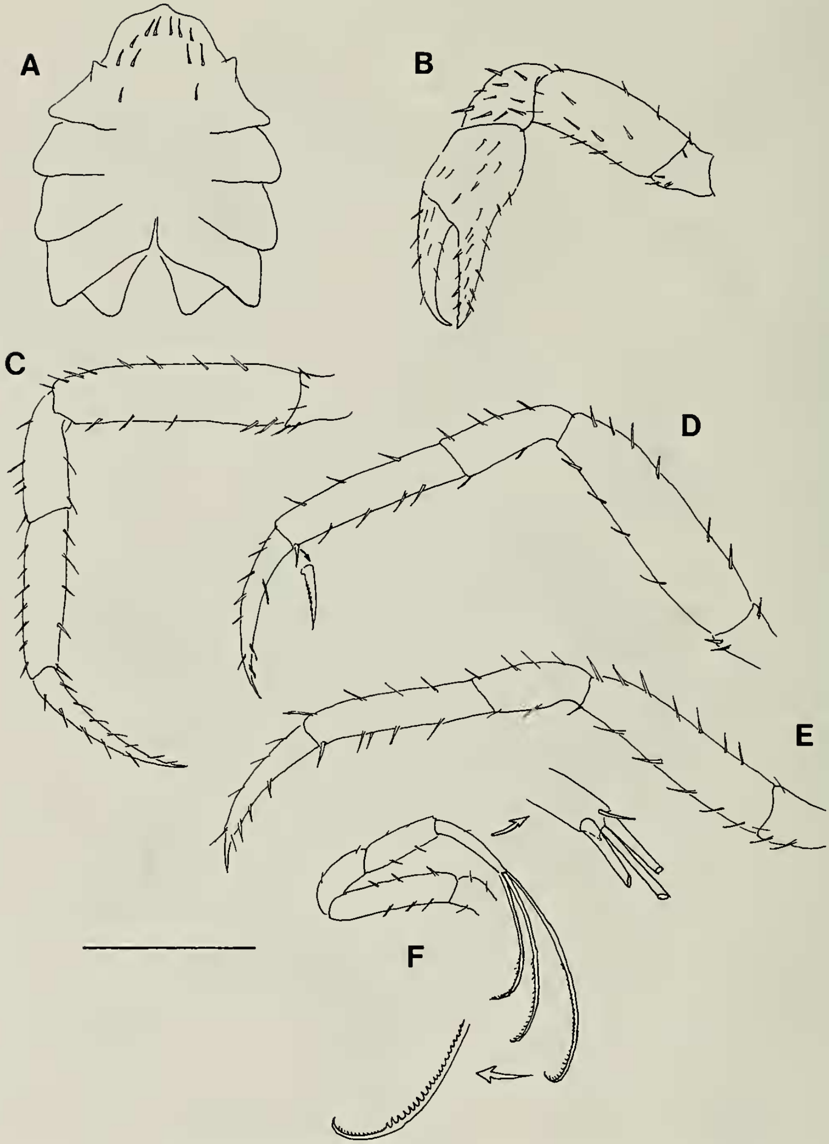

Fig. 4. *Chasmagnathus granulatus* Dana, 1851. Megalopa. A, sternal plate, ventral view; B–F, pereiopods 1–5, ventral view (B, F) and dorsal view (C–E). Scale bar = 0.5 mm.

setae. Somite 3–5 with 4 pairs of mid-dorsal setae. Somite 6 with 1 pair of mid-dorsal setae. Somites 2–5 with 1 pair of biramous pleopods (Fig. 5B–E), endopod unsegmented with 3 terminal hooks, exopod unsegmented, pleopods 1–4 with 16, 16, 15, 14 long marginal plumose natatory setae respectively. Uropods (Fig. 5F) 2-segmented on somite 6, proximal segment with 1 long marginal plumose natatory seta and distal segment with 9 long marginal plumose natatory setae.

Telson (Fig. 5A). —Squared in shape and rounded terminally, with 3 pairs of mid-dorsal setae, 1 pair of dorsolateral setae and 3 posterior marginal seta.

Morphometry

The length of cephalothorax, propodus of cheliped and first pleopod were significant-

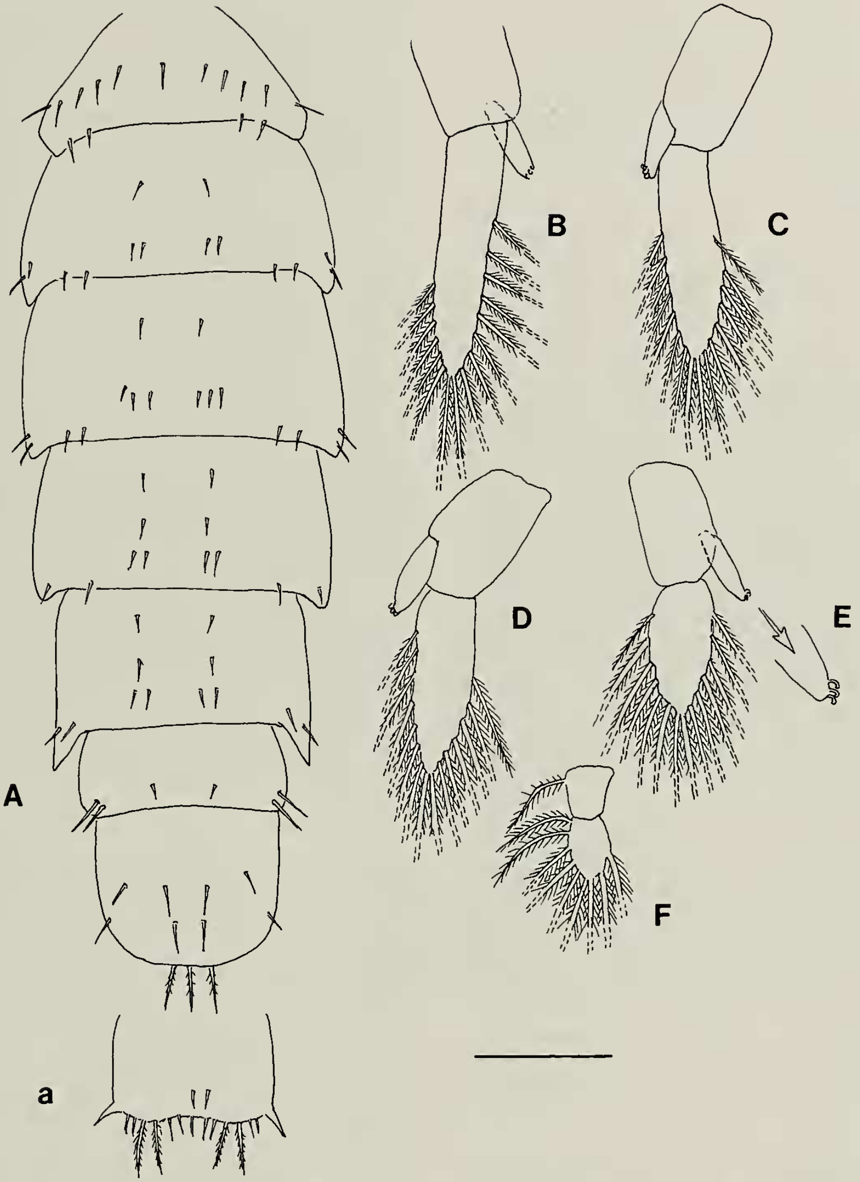

Fig. 5. *Chasmagnathus granulatus* Dana, 1851. Megalopa. A, abdomen, dorsal view; a, anomalous telson; B–E, pleopods; F, uropod. Scale bar = 0.2 mm.

ly larger in Samborombón Bay megalopae than Mar Chiquita Lagoon megalopae (Table 1).

Anomalous Megalopae

Several specimens from Mar Chiquita samples were found that do not show the general morphology and setation pattern for typical megalopal stages of *Chasmagnathus granulatus*, but clearly belong to this species. This was confirmed after successful moults into first crab were obtained in the laboratory. These specimens had the essential features of "normal" megalopa but exhibited the following variances: cephalotorax with different shape, bearing vestiges of

Table 1.—Morphometric comparison for megalopae of *Chasmagnathus granulatus* from Mar Chiquita Lagoon and Samborombón Bay, Argentina.

	Cephalothorax		Propodus of chelae		First pleopod length (mm)
	Width (mm)	Length (mm)	Height (mm)	Length (mm)	
Mar Chiquita					
n = 54	1.08 ± 0.08	1.27 ± 0.07	0.24 ± 0.01	0.57 ± 0.02	0.51 ± 0.02
Samborombón					
n = 25	1.12 ± 0.06	1.33 ± 0.06	0.24 ± 0.01	0.61 ± 0.03	0.53 ± 0.02
Student *t* Test	ns	P < 0.0001	ns	P < 0.0001	P < 0.0001

zoeal lateral spines, and a reduced number of setae (Fig. 1C), antennular peduncle with remains of exopodal and protopodal processes as spines (Fig. 2b), endopod of maxilla with setation 2, 2, as in the zoeal maxillar endopod (Fig. 2e), endopod of first maxilliped not simple, with few terminal setae, but elongated, not segmented, and with a number of setae and arrangement similar to those of zoeal stages (Fig. 3a), telson with two short terminal spines in place of furcal arms and a variable number of terminal processes (Fig. 5a).

Discussion

Descriptive comparison.—The present description for megalopae of *Chasmagnathus granulatus* differs from that of Boschi et al. (1967) in several features (Table 2). Clear differences can be observed in the setation pattern of several appendages. The setation of the coxa and basis of maxillules, maxillae and maxillipeds was not described by Boschi et al. (1967), nor was the setation or spinulation of pereiopods and abdomen.

Based on the zoeal and megalopal char-

Table 2.—Differences between previous (Boschi et al. 1967) and present description for megalopae of *Chasmagnathus granulatus.* Abbreviations: s., setation; a, aesthetascs; lm, lateral margin.

	Boschi et al. (1967)	Present study
Antennule		
Peduncle s.	not described	4, 3, 1
Endopod s.	3 (terminal)	1(subterminal) + 3(terminal)
Exopod (flagellum) a+s	not counted	0 + 0, 3 + 0, 4 + 2, 4 + 2
Antenna s.	0, 0, 0, 0, 0, 2, 2, 2, 2, 4	5, 2, 2, 0, 0, 4, 1, 4, 3, 3
Maxilla		
Scaphognathite lm s.	3 + 0	3 + 2
First maxilliped		
Epipodite s.	6–7	8
Exopod s.	4 (terminal)	2(terminal), 4(terminal)
Second maxilliped		
Epipodite s.	3–4	5
Endopod s.	1, 0, 3, 9–10	1, 1, 1, 6, 9
Third maxilliped		
Epipodite s.	14–16	20
Protopod s.	12–13	19
Endopod s.	11, 4–6, 0, 6–7, 5–6	14, 11, 8, 8, 8
Pleopod s.	17, 17, 15, 15	16, 16, 15, 14
Uropod s.	8–9	1, 9

acters proposed as typical for the family Varunidae by Cuesta et al. (2000), *Chasmagnathus granulatus* should be considered a varunid rather than a sesarmid species. Varunid characters for the megalopal stage are: 7 segments on the antennal flagellum, 3 + 2 lateral setae on the scaphognathite of the maxilla, dactylus of pereiopods 2–5 without denticulation on the inner surface, in some cases only strongly spinulate, and 8–19 setae on the distal segment of the uropod. All these characters are found in megalopae herein described for *C. granulatus.* In addition, this species does not exhibit typical features of sesarmid megalopae (Cuesta 1999), such as the absence of an antennular endopod and the presence of only four terminal setae on the mandibular palp. Also, the zoeal morphology of this species, as described by Boschi *et al.* (1967) (revised and corrected by Cuesta 1999, Cuesta et al. 2001), is clearly of a varunid. The above mentioned characters, along with recently reported mtDNA sequences and new adult morphological features (Schubart et al. 2000, 2002), support reassignment of *C. granulatus* to the family Varunidae.

Anomalous megalopae.—All the characters present in anomalous *C. granulatus* megalopae are clearly remains of zoeal stage features. There are other similar cases reported in the literature, many of them belonging to grapsoid species (Table 3), but in most cases these features were described as the common morphology and were not considered as anomalies. In all these examples, the material was reared in the laboratory and the obvious explanation was that they were laboratory artifacts. The present study shows that these anomalies can occur also in the natural environment, and a new explanation of their occurrence is thus needed.

The number of zoeal stages varies among different crab families. Some families have a constant number of zoeae (e.g., Majidae, two stages) but this number varies among genera of other families, and even among

Table 3.—Anomalous morphological features in the megalopal stage of six species of Grapsoidea. Abbreviations: (−) normal morphology; ?, no data.

	Armases cinereum	*Armases angustipes*	*Aratus pisonii*	*Sesarma reticulatum*	*Gecarcinus lateralis*	*Chasmagnathus granulatus*
Cephalotorax	(−)	(−)	Dorsal spine rudiment	Rostral spine directed anteriorly	(−)	Lateral spines rudiment
Antennal peduncle First segment	(−)	Well developed protopod and exopod	Protopod present	Exopod present	Protopod and exopod present	Protopod and exopod rudiment present
Maxilla endopod	2, 3	1, 3	2, 3	2, 2	2, 2	2, 2
First maxilliped Endopod	Elongated, with long setae	(−)	?	Elongated, segmented with long setae	Elongated, with long setae	Elongated with long setae
Telson	(−)	Short furcal arms present	Long furcal arms present	Long furcal arms present	Short furcal arms present	Short furcal arms present
Reference	Costlow & Bookhout 1960	Cuesta & Anger 2001	Warner 1968	Costlow & Bookhout 1962	Willems 1982	Present study

species of the same genus (e.g., Grapsoidea and Xanthoidea). Furthermore, other decapod crustaceans show variations in the number of developmental stages within a species, and this has been described as developmental plasticity (e.g., Caridea, see Knowlton 1974). This plasticity of developmental pathways has not been reported extensively in the Brachyura (see Montú et al. 1990 for a review), but it does occur in at least a number of grapsoid species. For example, the number of zoeal stages varies in *Cyclograpsus integer* H. Milne Edwards, 1837 (5 or 6) (by Gore & Scotto 1982), *Aratus pisonii* (H. Milne Edwards, 1853) (2, 3 or 4) (by Díaz & Bevilacqua 1986, 1987), *Chasmagnathus granulatus* (4 or 5) (by Pestana & Ostrenski 1995), *Armases rubripes* (Rathbun, 1897) (4 or 5) (by Montú et al. 1990), and *Eriocheir sinensis* H. Milne Edwards, 1853 (5 or 6) (by Anger 1991). The presence of anomalous megalopae occurrs in *Armases cinereum* (Bosc, 1802) (by Costlow & Bookhout 1960), *Sesarma reticulatum* (Say, 1817) (by Costlow & Bookhout 1962), *Aratus pisonii* (by Warner 1968), *Gecarcinus lateralis* (Freminville, 1835) (by Willems 1982), *Armases angustipes* (Dana, 1852) (by Cuesta & Anger 2001), and *C. granulatus* (this paper) (see Table 3). *Aratus pisonii* and *C. granulatus* are two of these "plastic" species previously listed; *S. reticulatum, A. cinereum* and *A. angustipes* belong to genera with a variable (two to four) number of zoeal stages among species.

In the laboratory, the occurrence of supernumerary zoeal stages and megalopal anomalies could be explained as a response to suboptimal conditions in food supply, temperature, salinity, or the synergetic effect of these. This explanation could also be extrapolated to the field, since these species usually inhabit unstable environments.

Mar Chiquita and Samborombón Bay saltmarshes are separated by about 200 km and have a similar climate. However, anomalous megalopae were found in Mar Chiquita, a shallow water coastal lagoon characterized by highly variable and unpredictable physical conditions (e.g., tidal level, salinity, Anger et al. 1994) but not in Samborombón Bay, a larger estuarine area with more regular tides and rather stable intermediate salinities (ca. 20‰). On the other hand, since Samborombón megalopae are larger, a differential environmental effect (e.g. food availability) on larval development cannot be ruled out. A differing larval export strategy was described for these two localities (Anger et. al. 1994): Mar Chiquita zoeae develop in coastal sea waters, whereas Samborombón Bay zoeae probably develop in richer waters of the mouth of Rio de la Plata.

The ecological and evolutionary significance of developmental plasticity in crabs is an interesting new area of research, but more experiments in the laboratory and the field will be necessary to fully interpret the significance of intermediate stages.

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